HYBRIDIZATION IN AMERICAN TRADESCANTIAS

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FOREWORD

Widely different opinions are held by present-day biologists as to the evolutionary importance of hybridization between species. One of the main reasons for the disagreement seems to be the lack of summarized and codified data bearing upon the problem. This series of papers is not an attempt either to prove or disprove the *importance* of hybridization. It is rather an attempt to gather pertinent data from which to analyze the *effects* of hybridization.

The genus *Tradescantia* has been chosen for two main reasons: (1) Previous taxonomic, cytological, and genetical studies (Anderson and Woodson, '35; Anderson and Sax, '36; Anderson, '36) have indicated the main outlines of the situation in this genus; (2) *Tradescantia* for purely technical reasons is a better object for such investigations than are many other genera of the higher plants, chief among its assets being the facility with which it can be studied cytologically and the ease with which most of the species can be brought into cultivation.

The main object of the investigation, as stated above, has been to procure data from which the importance and the evolutionary rôle of hybridization could be estimated and demonstrated. It had previously been experimentally determined that most of the species allied to *T. virginiana* could be hybridized and that their hybrid progeny were semi-fertile. Similar hybrids had been found in the field and had been subjected to detailed morphological and cytological analysis, but such work was purely preliminary. It merely demonstrated the occurrence of hybridization. What was needed was a method which would determine the dynamics of hybridization in natural populations. In mathematical terms it was necessary to ascertain the frequencies as well as the range of variation (Anderson and Turrill, '35). That is to say, that we needed to measure and record the effect of hybridization upon the entire population in which it was occurring. Such a method has been evolved and is outlined in section I, while its application to a particular case is demonstrated in section II.

I. A Method for Measuring Species Hybrids

Biology employs two methods of measurement, the quantitative and the qualitative. Each has its advantages and disadvantages. Two of the main objections to purely quantitative methods are: (1) quantitative scales are arbitrary and may not bear a direct relation to the phenomenon under investigation, (2) the observational basis of purely quantitative methods is too narrow for many biological problems. It may be well to amplify these *dicta*.

(1) The chief purposes of the quantitative method are to record the variation of certain phenomena and from this record to analyze the forces producing the variation. If a scale has been chosen which is an accurate reflection of the main underlying factors, then the analysis will be a comparatively simple matter. But if the scale used is not in harmony with these underlying causes then it may be difficult, or impossible, to analyze the data. In other words, the data are then no more than a record; a qualitative measure, if objectively defined, would have been quite as efficient. In a paper of fundamental biological significance Wright has demonstrated ('26) how even as simple a transformation as a percentage scale can obscure the interpretation of quantitative data. In many biological problems the customary quantitative scales in which the original observations are recorded are even more inefficient and misleading. The fact that centimeters are equally spaced on the ruler does not mean that variations of a centimeter are always of equal biological magnitude when we use that ruler to measure plants and animals. Purely quantitative measures, lengths, areas, weights, etc., are superior to qualitative units only when they reflect more or less directly the changes in the underlying factors.

(2) As has been pointed out by Minot ('11), the observa-

tional basis of purely quantitative methods is often too narrow for studying biological phenomena. A set of weights, or lengths, is too insignificant an observation to yield sufficient data for exploring a problem. Biology has advanced most rapidly when appropriate qualitative measures have been developed and used with precision. In Genetics, for example, the fundamental data are qualitative. Once obtained they are treated with such precision that most geneticists probably think of their work as purely quantitative. But the fundamental categories, "vestigial" vs. "non-vestigial," "scute" vs. "non-scute," "forked" vs. "non-forked," etc., are quite as qualitative as the fundamental categories of taxonomy. It is because of this fact that they are a broad enough tool to yield useful information about such a complex phenomenon as heredity. If the methods of Drosophila genetics were purely quantitative the flies would not be classified in qualitative categories, but their wing lengths, eye diameters, etc., would be laboriously measured. Imagine the difficulties of conducting a Drosophila experiment involving two or three wing mutants in which the only available data were the lengths and breadths of the wings! Genetics has been able to advance because it was willing to take the Mendelian recessive (a qualitative unit about whose ultimate significance relatively little was known) and to use that unknown but recognizable entity as a basic unit.

For the study of the species problem a similar combination of qualitative and quantitative methods seems desirable. Few of the differences between species are of the simple sort which are readily amenable to quantitative treatment (Anderson and Whitaker, '34). This is not to say that species do not differ quantitatively. They do, just as do the wing mutants of Drosophila, but in both cases it is more efficient to use qualitative categories.

Purely qualitative methods, however, have their own disadvantages. They are often said to be more subjective, but this point is open to argument. Certainly the gene differences by which Drosophilae are scored are quite as objective as quantitative measurements. A very real disadvantage in purely qualitative work is that it is not commensurate. One cannot with purely qualitative methods make an accurate comparison of the *Iris* plants of one meadow with those of another. What we need for the species problem is a method whose fundamental observations are based upon the qualitative categories of taxonomy but which treats these categories in such a way that they can be used for comparison and analysis. This has been done below in a fairly simple fashion by constructing an index which is the resultant of all the qualitative characters which are readily available.

In the simplest possible case the method operates as follows: Given two species, A and B, the hybridization between which is the object of investigation. Given n readily ascertainable differences between A and B (as, for instance, position of inflorescence, nature and distribution of pubescence, number of nodes to the stem, distribution of stomata, etc.). For each of these characters an individual plant can be scored as 'a' (like species A); as 'b' (like species B), or as 'i' (intermediate, preferably the actual F_1 if that has been obtained). In particular cases it will be possible to define two or more intermediate grades for the character in question. A hybrid population will be scored somewhat as follows in a case where six distinguishing characters were available:

plant no. 1: a-a-a-i-a-a
plant no. 2: a-a-i-i-b-i
plant no. 3: i-i-i-i-i-i
plant no. 4: b-i-i-i-b-a

and so on for all the plants which are scored. To summarize the population as a whole, all that is necessary is to turn this qualitative scoring into a quantitative index. An index running from complete "A-ness" to complete "B-ness" can be made by arbitrarily giving every 'a' the value of 0, every 'b' the value of 2, and every 'i' the value of 1. This will produce a scale with $2n + 1$ divisions (in this case 13, i. e., 0 to 12 inclusive. An individual of species 'A' would have an index value of 0 $(0 + 0 + 0 + 0 + 0 + 0)$, while an individual of species 'B' would have a value of 12. Plant no. 1 in the above example will have an index value of 1; plant no. 2 a value of 5; plant no. 3 a value of 6; plant no. 4 a value of 7. When the values of each plant have been computed they can be summarized as a frequency distribution. The frequency distribution constitutes a record of the whole population, in so far as these two species and mixtures between them are concerned. It can be used for the comparison of different hybrid populations and to discover and analyze the forces which are at work in such populations. The index can be varied to fit the available data in various ways. When, for instance, certain of the categories are thought to be more or less reliable than the others they can be appropriately weighted in combining the index. The method seems capable of producing useful and unique data in regard to the variation within and between species. I have used it extensively in the genus *Tradescantia,* one case being published in the second part of this paper. I have also applied it successfully to the analysis of hybridization in *Amelanchier* and *Baptisia* (unpublished). Dr. H. P. Riley has applied it to the hybrid *Iris* populations of the Mississippi delta with interesting results (Riley, in press).

After I had originated the method Dr. Jens Clausen very kindly called my attention to a paper by Raunkiaer ('25) in which an almost identical method of recording the qualitative categories had been applied to a case of hybridization in *Crataegus.* He had not, however, performed the further step of turning the qualitative record into an index, thus making it possible to summarize the population. When this is done the case proves to be a particularly interesting one with certain unique features.

SUMMARY

The advantages and disadvantages of quantitative and qualitative methods in biology are discussed. A method of summarizing hybrid populations is developed which utilizes qualitative categories for its initial observations and from these computes a quantitative index value.

II. Hybridization between T. virginiana and T. canaliculata

The method developed in Section I has already been applied to numerous cases of hybridization in *Tradescantia.* The following one has been selected for preliminary demonstration because it has been analyzed in greater detail and because it is a relatively simple case with no such complicating factors as differences in chromosome number.

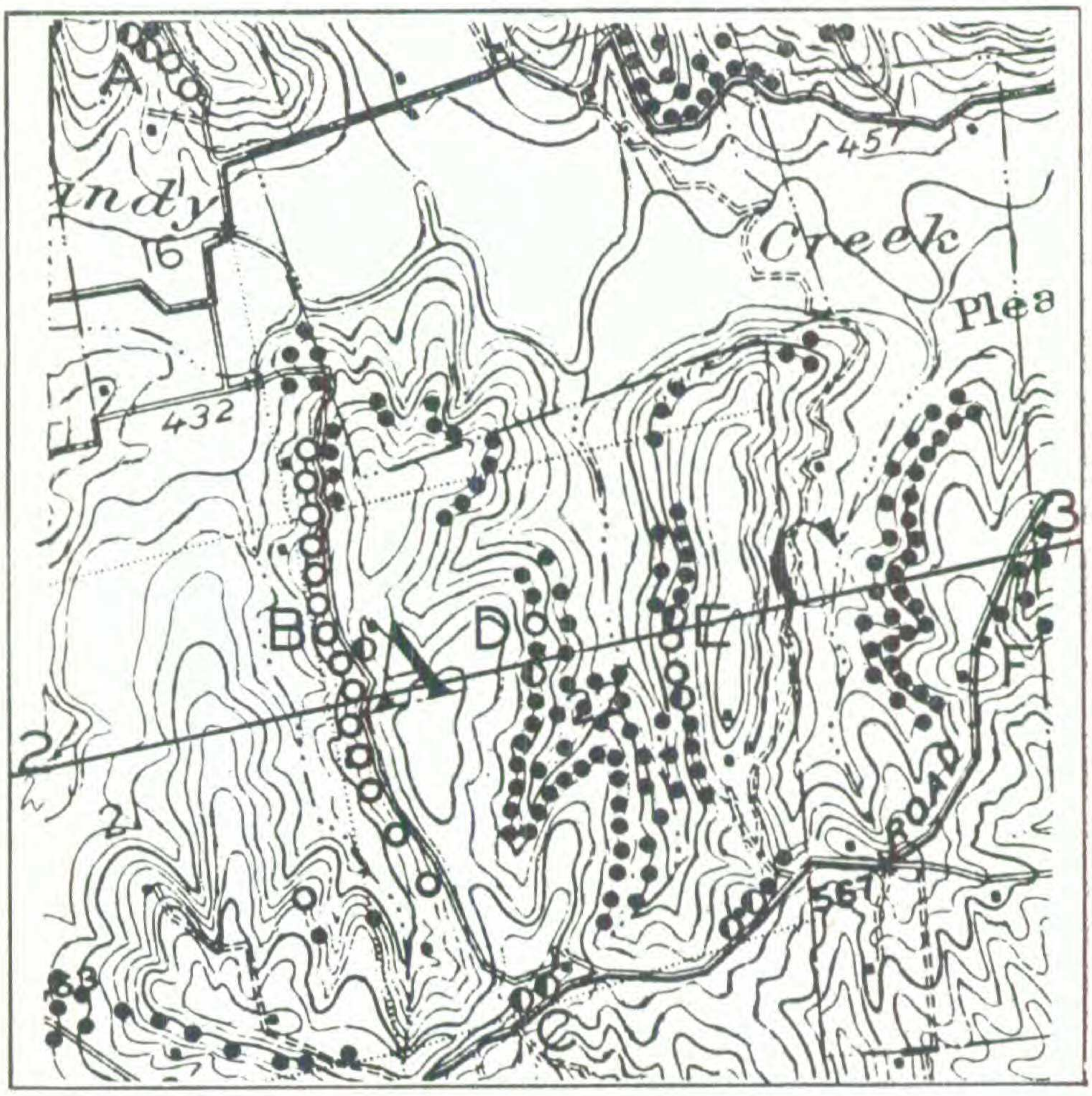
Tradescantia virginiana L. and *T. canaliculata* Raf. *(T. reflexa* Raf.) are the two commonest Tradescantias of eastern North America. Although each can be cultivated under a variety of conditions they are usually found growing naturally in quite different situations; *T. canaliculata* in the sun, often upon or near rocks or in dry sands; *T. virginiana* in shade or semi-shade. Until white civilization disturbed their natural relationships they seldom or never occupied the same habitat. Even at the present time active hybridization is confined to a very small proportion of either species. The outstanding morphological differences between the two species are as follows (those characters marked with an asterisk * require the use of a good hand-lens):

	T. virginiana	Index value	*T. canaliculata*	Index value
(1)	2–3 nodes	2	6–8 nodes	0
(2)	Sepals broadly ovate, apex broadly acute; calyx inflated after anthesis	2	Sepals elliptic, apex narrowly acute; calyx not inflated after anthesis	0
(3)	Sepals and pedicels pubescent throughout	3	Pedicels glabrous; sepals glabrous or barbate	0
(4)	* Stomata no more conspicuous than the cells of the upper epidermis	1	* Stomata (and subsidiary cells) much more conspicuous than the cells of the upper epidermis	0
(5)	* Stomatal areas of the upper epidermis narrower than the areas without stomata	1	* Stomatal areas much broader than the areas without stomata	0
(6)	* Longitudinal distance between stomata longer (often several times as long) than the diameter of a stoma	1	* Longitudinal distance shorter than the diameter of a stoma	0
	Total index value	10		0

It was a relatively simple matter to turn these characters into an index, according to the method developed in section I. The figures to the right show in each case the index value assigned to that character. In the case of (3) it was possible to recognize two intermediate grades. If the pedicel was weakly pubescent and the calyx showed the beginnings of a barbate tuft at the apex it was scored as 'vi' (virginiana-intermediate) with an index value of 2; if it had a strongly developed barbate tuft with scattered hairs on the calyx it was scored as 'ci' (canaliculata-intermediate) with an index value of 1. Categories (4), (5), and (6) are given only half the weight of the previous three since they are all different measures of the same quality, the distribution of stomata on the upper epidermis.

It is certainly true of *Tradescantia,* as Wiegand ('35) has observed for *Amelanchier,* that hybridization is much more frequent in areas greatly disturbed by man than under more natural conditions. For that reason an area was chosen for detailed examination in which hybridization between *T. virginiana* and *T. canaliculata* was for the most part taking place under nearly natural conditions. The spot finally chosen is illustrated in Map 1. It is an area two miles square in the township of Joachim, in Jefferson County, Missouri. After the area had been selected it was visited repeatedly by foot and by automobile in an effort to record the exact distribution of all the Tradescantias within the four square miles selected. The region is a low plateau, very much dissected by small streams which flow into the near-by Mississippi River. The land has been under cultivation for over a hundred years, the flat hill-tops (plateau remnants) and the rich valley bottoms being for the most part in cultivated crops while the steeper hillsides are left as woodlands or as woodland pasture. The underlying rocks are sedimentary and lie in practically the positions in which they were deposited with little faulting, folding, or tilting. All the strata are limestone with the exception of the St. Peter's Sandstone, here a soft gray-white stone usually exposed as a more or less perpendicular cliff capped with resistant limestone.

The stratigraphy is of considerable importance to the problem in hand, for it is these steep limestone and sandstone cliffs which constitute the natural habitat for *T. canaliculata.* They are so rocky and dry that not even in the original forest were they fully covered with trees, particularly on southern and western slopes. It will be seen on the map and in fig. 1 that



Map I. Distribution of *T. virginiana* (small closed circles), *T. canaliculata* (large open circles), and hybrids (black and white). The letters A to F indicate places at which detailed collections were made. The line 2–3 represents the position of the section illustrated in fig. 1.

T. canaliculata is confined to this narrow belt just below the hill-tops, while *T. virginiana* occurs pretty generally throughout the region on gentle slopes, on hill-tops, and in valley bottoms, but practically always in the shade.

In this particular area *T. virginiana* was much more common than *T. canaliculata.* An effort was made to estimate relative frequencies by computing from the map the areas occupied by

T. virginiana, T. canaliculata, and the hybrids. These were found to be 16 : 1 : 0.5 respectively.

Thirty plants each of *T. virginiana* and *T. canaliculata* were scored at the localities marked as 'F' and 'B' on the map. The pure species, as can be seen from table I and fig. 2, were relatively invariable and agreed with scorings made at other points in their range. A few hybrid plants were found along the zone of contact between the two species and large hybrid colonies, consisting of fifty or more individuals, occurred at four places, labeled A, C, D, and E on the map. Detailed studies were made at the first two localities.

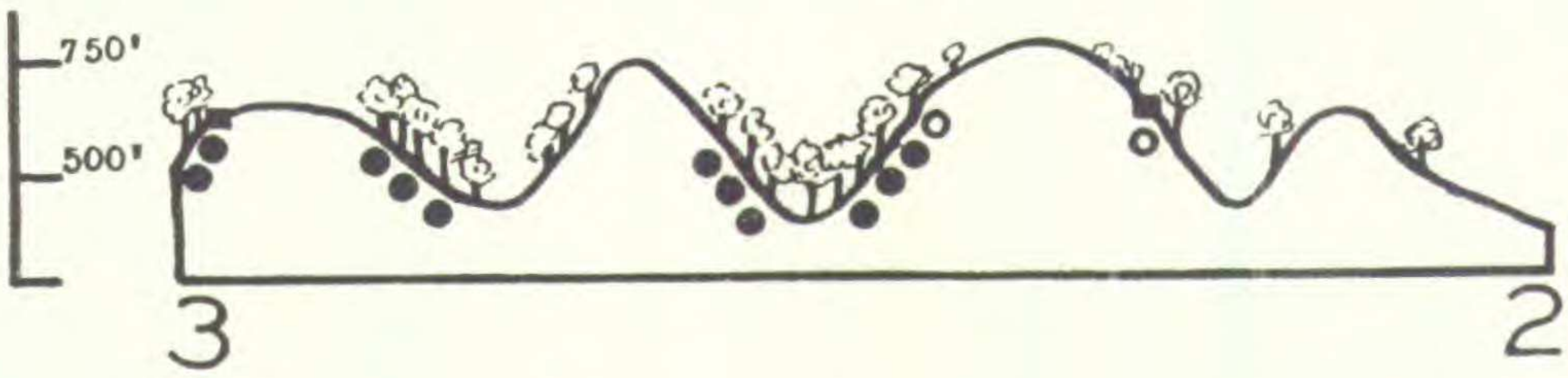


Fig. 1. Diagrammatic section (to scale) along line 2–3 in Map I. Figures to the left show feet above sea-level; closed circles represent *T. virginiana* and open circles *T. canaliculata.* The line is slightly over 2 miles long.

Locality A. At this point the public road starts up onto Sandy Ridge along the hard limestone which caps the St. Peter's Sandstone. The latter forms a series of much-weathered cliffs slightly to the south of the road and while the area is pastured, it has not been greatly disturbed of late years. At various points along the cliff a few plants of *T. canaliculata* are growing, and as the road swings to the right the cliffs and the ledge become somewhat shadier by reason of the narrow gorge cut back into the hill by an intermittent stream. At the head of the gorge there is an interesting area of a few hundred square feet in which many kinds of habitats and hence many kinds of plants are brought into close juxtaposition. Rock-plants, prairie grasses, woodland and even desert species are found within a few feet of each other. It is, in other words, exactly the situation in which one might logically expect to find hybridization between ecologically isolated species. Trades-

TABLE I

SCORING OF INDIVIDUAL PLANTS AT THREE LOCALITIES IN JEFFERSON COUNTY, MISSOURI. FURTHER EXPLANATION IN TEXT.

Plant no.	Categories (1)	(2)	(3)	(4)	(5)	(6)	Total	Plant no.	Categories (1)	(2)	(3)	(4)	(5)	(6)	Total
Locality B—*T. virginiana*															
1	v	v	v	v	v	v	11	16	v	v	v	v	v	i	10½
2	v	v	v	i	v	v	10	17	v	v	v	v	v	v	11
3	v	v	v	v	v	v	11	18	v	v	v	v	v	v	11
4	v	v	v	i	i	v	9½	19	v	v	v	v	v	v	11
5	v	i	v	v	v	v	10	20	v	v	v	v	v	v	11
6	v	v	v	v	v	v	11	21	v	v	v	v	v	i	10½
7	v	v	v	v	v	v	11	22	v	v	v	v	v	v	11
8	v	v	v	i	v	v	10	23	v	v	v	v	v	v	11
9	v	v	vi	i	v	v	9	24	v	v	v	v	v	v	11
10	v	i	v	v	v	v	10	25	v	v	v	v	i	v	10½
11	v	v	v	v	v	v	11	26	v	v	v	v	v	i	10½
12	v	i	v	v	v	i	9½	27	v	v	v	v	i	v	10½
13	v	v	v	v	i	v	10½	28	v	v	v	i	v	i	9½
14	v	v	v	v	i	v	10½	29	v	v	v	v	v	v	11
15	v	v	v	v	v	v	11	30	v	v	v	v	v	v	11
Locality F—*T. canaliculata*															
1	c	c	c	c	c	c	0	16	c	c	c	i	i	c	1½
2	c	c	c	c	i	c	½	17	i	c	c	c	c	c	1
3	c	c	c	c	c	c	0	18	c	c	c	i	c	c	1
4	c	c	c	c	i	c	½	19	c	c	c	i	i	c	1½
5	c	c	c	c	c	c	0	20	i	c	c	c	c	c	1
6	i	c	c	i	c	c	1½	21	c	c	c	c	i	c	½
7	c	c	c	i	c	c	1	22	c	c	c	c	c	c	0
8	c	c	c	i	i	c	1½	23	c	c	c	c	c	c	0
9	i	c	c	c	c	c	1	24	i	c	c	c	c	c	1
10	i	c	c	c	c	c	1	25	i	c	c	c	i	c	1½
11	c	c	c	c	c	c	0	26	c	c	c	c	c	c	0
12	c	c	c	c	i	c	½	27	c	c	c	c	c	c	0
13	c	c	c	c	c	c	0	28	c	c	c	i	c	c	1
14	c	c	c	i	c	c	1	29	i	c	c	c	c	c	1
15	c	c	c	i	c	c	1	30	c	c	c	c	i	c	½
Locality A—*T. virginiana* x *T. canaliculata*															
1	v	c	ci	c	i	v	3½	16	i	i	vi	i	i	i	6
2	i	c	ci	c	i	c	2½	17	c	c	ci	v	i	i	4
3	i	c	vi	c	i	c	3½	18	i	c	ci	c	i	i	3
4	i	c	ci	c	c	c	2	19	i	i	vi	c	i	i	5
5	i	c	ci	i	i	i	5	20	i	c	ci	i	i	c	3½
6	i	i	vi	c	i	i	5	21	i	i	ci	v	v	c	6
7	i	i	c	c	c	i	2½	22	i	i	vi	v	v	i	9½
8	i	i	ci	v	c	v	6	23	i	c	vi	i	i	c	4½
9	i	c	ci	c	c	i	2½	24	i	i	vi	v	v	i	7½
10	i	c	c	i	i	c	2½	25	i	c	v	i	i	c	5½
11	i	v	ci	c	i	i	5	26	c	c	vi	v	c	i	4½
12	i	v	vi	c	i	i	5	27	i	v	vi	v	v	i	8½
13	i	c	ci	i	i	c	3½	28	i	i	v	c	i	v	6½
14	i	i	c	c	i	i	3	29	i	i	v	v	v	i	7½
15	c	i	c	c	i	c	1½	30	i	c	c	v	c	c	3

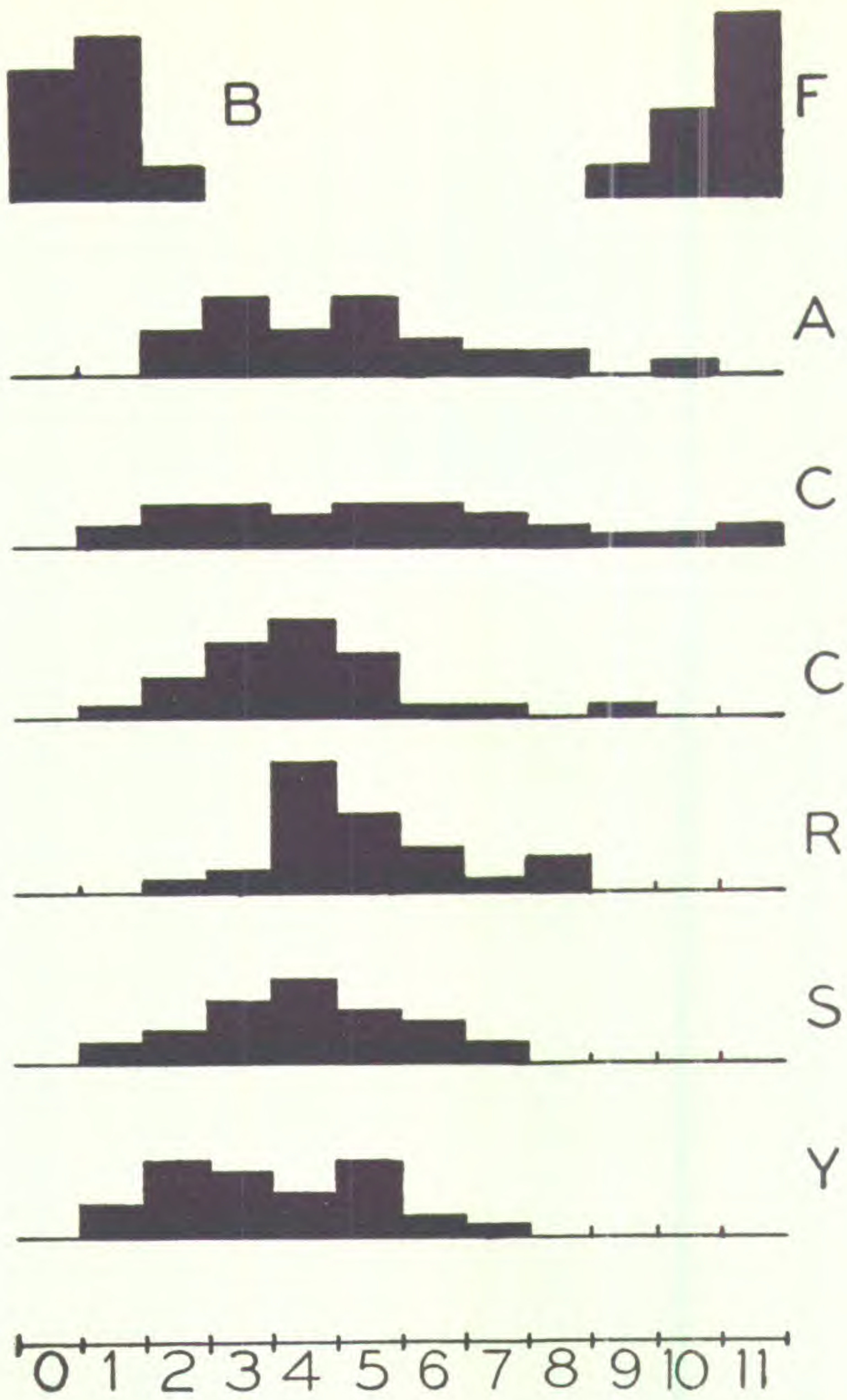


Fig. 2. Frequency distributions for the *virginiana-canaliculata* index. Thirty plants each collected at localities A, B, C (two terraces), and F illustrated in Map I; R and S at Algonquin Station, Y at Maplewood, Missouri. Index values shown on the scale at the base of the diagram. B represents a population of pure *T. canaliculata*, F a population of pure *T. virginiana;* the remainder hybrid populations. Further explanation in the text.

cantias occur rather generally over the whole area; a few plants of apparently straight *T. virginiana* are growing in the shade of the red cedars and a mongrel population of *T. virginiana* × *T. canaliculata* grows in the sunny and semi-shady situations. The cliff at this point is so steep that it was impracticable to collect plants in quantity from the cliff-sides but all of those growing on the ledge were scored in detail. The results are presented in table I and fig. 2, A. (In presenting the frequency distributions only the first thirty plants have been

SCALE VALUE	1-2	3-4	5-6	7-8	9-10
0-1			1		
2-3	2	1	2	4	4
4-5	2	5	2	4	3
6-7	5	4		2	2
8-9				2	

LIGHT INTENSITY

Fig. 3. Correlation between scale value and the light intensity of the habitat for 46 hybrid plants at locality A. Light intensity in parts of a second required for an equivalent exposure (i. e., scale runs from very shady at left to full sun at the right).

utilized in order to facilitate frequency comparisons with the other distributions.)

The peculiar frequency distribution exhibited by the hybrids at locality A has been found to be generally characteristic of hybrid colonies of *T. canaliculata* × *T. virginiana*. It can be conveniently, if somewhat loosely, described by saying that in such populations the hybrids "absorb" the *T. canaliculata* completely but that *T. virginiana* tends to persist in a more or less pure state. It will be seen from fig. 2 that there are no absolutely pure *T. canaliculatae* in spite of the fact that the bulk of the population is much closer to that species than to *T. virginiana*. These must largely be plants which are ¾ or

$7/8$ or $15/16$ *T. canaliculata.* At the other end of the scale there is a small proportion of *T. virginiana* but very few or none of the $3/4$, $7/8$, and $15/16$ *T. virginiana.* As to why the two species should react in this matter one cannot as yet even hazard a guess. Since most of the hybrid populations made up of these two species react in about the same fashion, the reason is probably internal. There seems to be some force or forces which inhibits free recombination between the hybrids and *T. virginiana* and encourages such recombination between the hybrids and *T. canaliculata.* It might possibly be differential pollen-tube growth; it might be a markedly different span of life (both species are perennial); it might be a result of the differences in blooming season (i. e. *T. virginiana* blossoms early and *T. canaliculata* blossoms late. If the hybrids very largely bloomed within the flowering period of the latter species it might produce the observed result).

Among the hybrids those morphologically most like *T. canaliculata* seemed to be growing in the sunniest locations and those most like *T. virginiana* in the shadiest. An attempt was made to measure this objectively and the results are presented in fig. 3 in the form of a correlation table between light intensity and index value. The former was measured with a light meter on a day of uniform cloudiness. The meter was held a foot above the inflorescence and gave readings in fractions of a second required for equivalent exposures. As will be seen from fig. 3, the results indicate that among the hybrids (the pure *T. virginiana* having been excluded) the deeper the shade the greater is the tendency to resemble *T. virginiana.*

At *Locality C* hybridization has produced very similar results. It is a less desirable spot for detailed study since it is adjacent to a state road whose position has been repeatedly shifted and the immediate environment in which the hybrids are found has been subject to violent alterations during the last half century. The cliffs at this point form a series of narrow terraces ten to twenty feet wide and several hundred yards in length. Where the hybrids occur each terrace has evolved a more or less characteristic type. Two collections made on the upper terrace at intervals of fifty feet gave nearly identical frequency distributions, while nearly adjacent collections from successive terraces showed different distributions. Natural selection is apparently working upon the hybrid population to produce these very local differences. Were this locality less subject to frequent and profound disturbances it would merit a much more detailed analysis.

Localities D and E were discovered too late in the flowering season to receive more than a preliminary survey. They apparently present the same general picture as did A and C.

Tradescantia virginiana and *T. canaliculata* also hybridize when growing as weeds along railroad rights-of-way, on vacant lots in the city, etc. Several such populations were examined in and near the city of St. Louis in the spring of 1936. Throughout this area *T. canaliculata* is the common weed *Tradescantia,* sometimes occurring along railroad embankments as the predominant plant of early summer for distances of several miles. Occasionally, however, in the immediate neighborhood of open oak woods, *T. virginiana* also contributes to the weed population. Two such hybrid colonies were investigated. Near the Algonquin Station of the Missouri Pacific Railroad two samples (R and S, fig. 2) of thirty plants each were collected between the railroad track and the highway. In Maplewood a sample of thirty (Y, fig. 2) was collected from a vacant lot adjacent to the electric railway. It will be seen that, as in the case of the collections made in Jefferson County, the bulk of the population is composed of individuals which score from 3 to 5 on the scale, individuals in other words which must be about ¾ to ⅞ *T. canaliculata.* Hybridization between *T. virginiana* and *T. canaliculata* both along the cliffs and the railroad tracks tends to produce a somewhat variable "*sub-canaliculata.*"

SUMMARY

Hybridization between *T. canaliculata* and *T. virginiana* was studied at seven localities in Missouri. At these localities there seemed to be a general tendency for the hybrids to "absorb" *T. canaliculata* though *T. virginiana* may persist in a pure state as a small percentage of the population. This is

interpreted as the result of a force or forces, as yet undetermined, which inhibit free recombination between the hybrids and *T. virginiana* and encourage such recombination with *T. canaliculata.*

A general discussion of hybridization is deferred until further cases have been investigated. From data already at hand it is apparent that hybridization, as previously suspected, is very widespread in the genus *Tradescantia.* The details differ somewhat with the conditions of the environment and very greatly according to the species taking part. In certain cases, at least, the resultant variability is so widespread throughout the species, that it must constitute the chief raw material for natural selection. As such it deserves exhaustive observation and critical analysis.

BIBLIOGRAPHY

Anderson, Edgar ('36). A morphological comparison of triploid and tetraploid interspecific hybrids in Tradescantia. Genetics **21**: 61–65.

————, and Karl Sax ('36). A cytological monograph of the American species of Tradescantia. Bot. Gaz. **97**: 433–476.

————, and W. B. Turrill ('35). Biometrical studies on herbarium material. Nature **136**: 986.

————, and T. W. Whitaker ('34). Speciation in Uvularia. Arn. Arb. Jour. **15**: 28–42.

————, and R. E. Woodson ('35). The species of Tradescantia indigenous to the United States. Arn. Arb. Contr. **9**: 1–132.

Minot, C. S. ('11). The method of science. Science **33**: 119–131.

Raunkiaer, C. ('25). Ermitageslettens Tjørne. Isoreagentstudier I. Kgl. Danske Videnskab. Selskab. Biol. Meddel. **5**: 1–76.

Wiegand, K. M. ('35). A taxonomist's experience with hybrids in the wild. Science **81**: 161–166.

Wright, Sewall ('26). A frequency curve adapted to variation in percentage occurrence. Jour. Am. Statistical Assn. **1926**: 162–178.